

Recent Replacement of Native Pili Grass (*Heteropogon contortus*) by Invasive African Grasses in the Hawaiian Islands¹

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ABSTRACT: We surveyed 41 sites from throughout O'ahu that had been dominated by native pili grass (*Heteropogon contortus*) in the late 1960s. Pili grass was absent from 14 (35%) of those sites in 1997 and had declined in abundance in most of the 27 remaining sites, relative to the late 1960s. The pili grass communities have been replaced by communities dominated by one of three African grasses: *Cenchrus ciliaris* (buffel grass), *Pennisetum setaceum* (fountain grass), or *Panicum maximum* (Guinea grass). *Panicum maximum* was often associated with the shrub *Leucaena leucocephala*, and *Cenchrus ciliaris* and *Pennisetum setaceum* communities showed little evidence of succession toward woody vegetation. Communities dominated by the African grasses were significantly less diverse, in terms of number of plant species, than the native pili grass-dominated communities. Observations made on other Hawaiian islands suggest that this rapid pili grass decline and replacement with alien grasses has not been limited to O'ahu. Research is needed to determine how higher-diversity native pili grass communities can be maintained in the Hawaiian Islands as a valuable natural and cultural resource.

PILI GRASS (*Heteropogon contortus* (L.) P. Beauv. Ex Roem. & Schult.) is a pantropical perennial grass that is indigenous to the Hawaiian Islands (Hitchcock 1922) or perhaps an early Polynesian introduction (Degener and Degener 1968). Pili grasslands are thought to have covered leeward coastal lowlands and hillsides of the Hawaiian Islands extensively before the 1700s (Hitchcock 1922, Vogl 1969). Pili grass has important cultural value as a preferred thatching material used by native Hawaiians (Degener and Degener 1968), and pili grasslands can also have high value as forage for cattle (Hitchcock 1922, Grice and McIntyre 1995). Extensive pili grasslands were described on O'ahu by F. Egler in the 1940s (Egler 1947),

and more recently, Kartawinata (1971) conducted phytosociological studies of pili grass communities on O'ahu.

Over the past 50 yr, anecdotal observations have suggested that pili grasslands are declining rapidly throughout the Hawaiian Islands (e.g., Wagner et al. 1990:1551); however, we are not aware of any studies that have quantitatively documented this apparent decline. Quantitative information on the extent and rate of pili grass decline, as well as on what has replaced pili grass, is needed to assess conservation concerns. In this study, we compared detailed descriptions of 41 pili grass-dominated communities from throughout O'ahu that were made by K. Kartawinata between 1965 and 1968 (Kartawinata 1971) with our present-day assessment of his original sites to quantify vegetation changes that have occurred over the past 30 yr. These data give an indication of the rate of pili grass decline since the late 1960s, while also revealing what has been replacing pili grasslands on O'ahu.

¹ Manuscript accepted 24 October 1997.

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MATERIALS AND METHODS

Relocating Plots

During June and July 1997, we resurveyed sites on O'ahu that were classified as *Heteropogon contortus*–*Rhynchelytrum repens* communities in Kartawinata's 1965–1968 surveys (Kartawinata 1971). All of these communities formerly were dominated by pili grass. Original sites were plotted onto U.S. Geological Survey topographic maps (1:24,000 scale) using the latitude and longitude coordinates as given in Kartawinata (1971). In some cases, upon arriving at the site coordinates, the precise plot locations were obvious from the physical description of the site, including landmarks, given by Kartawinata. For sites with less-specific descriptions, we first located the correct latitude and longitude, and we then matched the altitude, slope, and exposure given by Kartawinata (1971) to find the specific site. Once at the correct altitude, slope, and exposure, we searched a 525-m² area around the site, looking for the area of highest pili grass density. We chose the area of highest pili grass density for our sample plots to ensure that our estimates of decline were conservative, because we could not be sure of the precise location of Kartawinata's original 100-m² sample plot within the community. Although the plot locations that we chose to sample may not have been the precise 100-m² plots sampled by Kartawinata, our plots likely fell within the boundaries of the original *Heteropogon*–*Rhynchelytrum* communities identified by Kartawinata, because the original communities were far more extensive than 100 m² (Kartawinata 1971).

In relocating the plots, we encountered some obvious errors in the latitude or longitude given by Kartawinata (1971). For example, some plot coordinates were in the ocean. In these cases, we used the site location (e.g., Wa'ahila Ridge), site description (soil, rock characteristics), altitude, slope, and exposure provided by Kartawinata to determine the correct latitude or longitude. Most errors were simply cases of transposi-

tion of numbers or errors in adding (or subtracting) from a known latitude (KLA) or known longitude (KLO) on a map. All site locations and characteristics, including corrected latitudes and longitudes, are given in the Appendix.

Sampling Method

Kartawinata (1971) used the Zürich-Montpellier method (Braun-Blanquet 1964, Mueller-Dombois and Ellenberg 1974) with 100-m² sampling units to quantify community composition. To be as consistent as possible, we followed the same methods. Kartawinata had previously determined that a 100-m² plot was the optimal size for sampling species in these dry grassland communities (Kartawinata 1971). A 100-m² plot was positioned within the area of maximum pili grass density at each of Kartawinata's relocated original sites, and percentage cover was estimated visually for major vegetation components. Percentage cover was then converted to the Braun-Blanquet (1964) scale, which has the following values: 5, showing cover >75%; 4, showing cover between 50% and 75%; 3, showing cover between 25% and 50%; 2, showing cover between 5% and 25%; 1, abundant but covering <5% plot area; +, several individuals, little cover; r, solitary with insignificant cover.

Analyses

All statistical analyses were conducted with the SYSTAT computer program (Wilkinson 1996). Pili grass abundances at sites sampled from 1965 to 1968 were compared with abundances in 1997 using the Wilcoxon signed-rank test (Daniel 1990) based on the cover-abundance classes for pili grass. The communities were classified using multidimensional scaling (MDS) based on the standardized species correlation matrix and using the Kruskal method (Wilkinson 1996). Rare species (those found in less than three plots or with a cover abundance of less than one in all plots) were excluded from

analysis to avoid spuriously high similarities among sites due to shared species absences (Ludwig and Reynolds 1988). Ten of the original *Heteropogon-Rhynchelytrum* communities sampled by Kartawinata between 1965 and 1968 were chosen randomly and plotted on the MDS axes for comparison with 1997 communities.

RESULTS

We relocated all 41 *Heteropogon-Rhynchelytrum* community sites originally surveyed by Kartawinata (1971). Two of the sites (1 and 2 near Koko Head) were not re-surveyed because houses had been built over them. When compared with the 1967 data, the remaining sites had significantly lower pili grass cover in 1997 (Table 1). Fifteen of the sites remained dominated by pili grass, but pili grass was completely absent from 14 sites. Among sites that retained some pili grass cover, the mean cover class score for pili grass was 4.2 in 1967 and 2.9 in 1997, a significant decline (Wilcoxon signed-rank test, $Z = -4.76$, $T = -27$, $n = 39$, $P < 0.001$). The pili grass has been replaced primarily by invasive African grasses.

Classification of sites using MDS accounted for 69% of variance among sites and distinguished several types of communities (Figure 1). All species used in the MDS analysis and their factor loadings are listed in Table 2. The vectors for several of the dominant species have been plotted on the MDS axes (Figure 1) to aid in interpretation. Sites clustering together in the right upper corner of the MDS plot were low-diversity communities dominated by *Cenchrus ciliaris*. Communities dominated by *Panicum maximum-Leucaena leucocephala* cluster broadly in the left upper corner, and *Pennisetum setaceum* communities can be seen loosely clustered around the center (0,0). The original 1967 pili grass-dominated plots cluster well together near the bottom center, and about a dozen 1997 sites overlap with the original sites (Figure 1). Species diversity

TABLE 1
COMPARISON OF PILI GRASS COVER ABUNDANCE IN 1967 AND 1997

SITE NO. ^a	PILI GRASS COVER IN 1967 ^b	PILI GRASS COVER IN 1997 ^b
3	4	2
4	3	3
5	3	4
6	3	5
13	5	3
30	4	0
43	5	0
44	5	0
45	3	0
46	4	0
47	4	0
48	3	0
49	5	2
50	3	5
53	4	2
55	3	0
58	2	0
64	4	2
65	5	2
73	3	3
78	5	3
79	5	4
80	5	0
81	5	3
89	5	4
91	4	2
92	5	+
93	4	0
94	4	0
96	5	2
97	5	5
98	5	3
99	5	3
100	5	5
101	3	4
102	4	2
103	4	0
104	5	1
105	5	0

^a See Appendix for description of sites.

^b See Materials and Methods for definitions of cover classes.

(total number of species encountered per 100-m² plot) averaged significantly lower in plots lacking pili grass (mean = 5.6 species) compared with plots that were dominated by pili grass (mean = 12.6 species; t -test, $t = 4.7$, $df = 22$, $P = 0.001$).

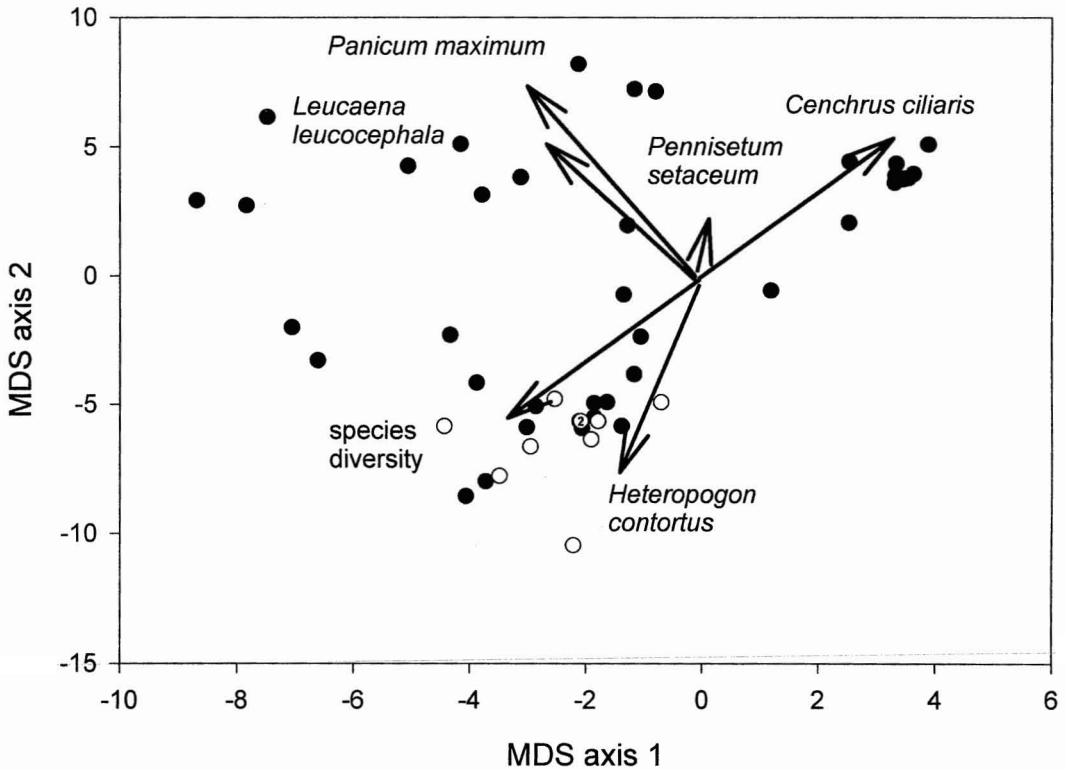


FIGURE 1. Classification of communities by multidimensional scaling. Dark circles are sites sampled in 1997. White circles are 10 randomly selected pili grass-dominated communities from 1965–1968. The point labeled “2” represents two superimposed data points. Vectors are plotted for dominants species, and vector lengths are proportional to species weights in the MDS analysis (see Table 2). Stress of the final configuration was 0.237.

DISCUSSION

Our reassessment demonstrates a transformation of over 33% of pili grass-dominated communities to African grass-dominated communities within the past 30 yr. In the approximately 66% of sites where pili grass was still present, it was usually considerably less abundant than in 1967. A few sites with increased pili grass abundance in 1997, relative to 1967, may have been an artifact of our conservative methodology of searching a large area around the site and choosing the 100-m² plot with the highest local abundance of pili grass. With the exception of a population at Koko Head, the largest pili grass-dominated communities that we encountered on O‘ahu were well under 500 m², clearly

only small remnants of what was present on rocky hillsides in the 1940s (Egler 1947).

African Grass Communities

Communities that have replaced pili grass are dominated by African grasses and can be classified into three types, based on the MDS analysis and observations. The *Cenchrus ciliaris*-dominated communities (12 sites) are primarily monocultures, typically with less than 5% cover each of *Sida fallax*, *Waltheria indica*, and *Leucaena leucocephala*. These were some of the lowest-diversity communities we encountered. *Cenchrus ciliaris* was first noted in the Hawaiian Islands in 1932 and is now found growing in dry habitats on

TABLE 2
SPECIES COMMONLY ENCOUNTERED IN RESURVEYED PLOTS
AND THEIR FACTOR LOADINGS ON
THE MULTIDIMENSIONAL SCALING AXES

SPECIES	MDS AXIS 1	MDS AXIS 2
<i>Acacia farnesiana</i>	-1.39	-0.1
<i>Cenchrus ciliaris</i>	0.82	0.86
<i>Chamaechrista nictitans</i>	0.74	0.33
<i>Chamaesyce hirta</i>	0.4	-0.87
<i>Chloris barbata</i>	0.46	-0.42
<i>Desmodium triflorum</i>	0.76	-0.23
<i>Emilia sonchifolia</i>	-0.02	-0.93
<i>Eragrostis variabilis</i> ^a	-1	0.56
<i>Heteropogon contortus</i> ^a	-0.33	-1.14
<i>Hyptis pectinata</i>	0.46	0.87
<i>Lantana camara</i>	0.99	-0.07
<i>Leucaena leucocephala</i>	-0.64	0.86
<i>Panicum maximum</i>	-0.71	1.17
<i>Passiflora foetida</i>	0.88	-0.47
<i>Pennisetum setaceum</i>	0.04	0.2
<i>Prosopis pallida</i>	0.45	0.73
<i>Rhynchelytrum repens</i>	-0.53	-0.98
<i>Sida fallax</i> ^a	-0.99	0.31
<i>Stapelia gigantea</i>	0.91	0.09
<i>Waltheria indica</i> ^a	-0.5	0.04

^aNative species.

all the islands (Wagner et al. 1990). The dry, rocky slopes formerly dominated by pili grass appear to be an ideal habitat for *C. ciliaris*, and the spread of *C. ciliaris* through these habitats over the last few decades must have been rapid, because Kartawinata (1971) only occasionally noted *C. ciliaris* at low abundances. *Cenchrus ciliaris* grows denser than pili grass and appears to pose a higher fire risk. A fire in a *C. ciliaris* community would be expected to spread faster and farther than in pili grasslands, where frequent open rock outcrops had provided barriers to the spread of fire (Mueller-Dombois 1981).

The second invasive African grass that has taken over pili communities is *Pennisetum setaceum* (three sites). *Pennisetum setaceum* was also found as nearly monospecific stands, often with *Waltheria indica* and *Chamaechrista nictitans* as minor components. *Pennisetum setaceum* was introduced to the Hawaiian Islands as an ornamental grass and makes a poor forage (Hosaka and Thistle 1954). On O'ahu, *P. setaceum* was just be-

ginning to escape from plantings in the 1940s (Egler 1947) and was only rarely seen by Kartawinata in the 1960s (Kartawinata 1971). Over the past 30 yr, *P. setaceum* has invaded extensively in the Lanikai area and has covered several of Kartawinata's original pili communities there. *Pennisetum setaceum* has also now escaped and is spreading in several other areas of southeastern O'ahu. Although we often found seedlings of the shrubs *L. leucocephala*, *Acacia farnesiana*, and *Lantana camara* in our plots, we rarely found juvenile (1 to 3 yr old) plants. Scattered adult shrubs surrounded by *P. setaceum* or *C. ciliaris* are likely to be remnants of a former community. The established *P. setaceum* and *C. ciliaris* grasslands appear to inhibit colonization by shrubs to any great extent, perhaps through competition with shrub seedlings for water. Our concern about increased fire frequency in *C. ciliaris* grasslands relative to pili grasslands also applies to the dense *P. setaceum* grasslands (Smith and Tunison 1992, Tunison 1992). *Pennisetum setaceum* and *C. ciliaris* thrive in similar habitats with respect to soil substrate and precipitation and are both currently spreading on O'ahu. Careful observations or experiments will be needed to predict the future extent of *C. ciliaris* versus *P. setaceum* grasslands on leeward coastal hills of the Hawaiian Islands.

The third African grass that was dominant in several former pili grass communities was *Panicum maximum*, a grass that has been cultivated in Hawai'i as a forage since the 1800s (Wagner et al. 1990). *Panicum maximum* is phenotypically variable and can range in end-of-season height from 50 to 300 cm, often depending on water availability. In our plots, *P. maximum* was typically less than 75 cm tall and was generally growing under or around the nitrogen-fixing shrub *Leucaena leucocephala*. Kartawinata (1971) noted an influence of *L. leucocephala* over time on soil development. He described thicker, richer (darker), and moister soils beneath established *L. leucocephala*, relative to surrounding substrates (see also Egler 1942). It is on these slightly better developed, moister soils that *P. maximum* seems to thrive. Kartawinata (1971) observed the association between *L. leucoce-*

phala and *P. maximum* in two sites, both located at an altitude of only 6 m. Since then, the *L. leucocephala*–*P. maxima* community has apparently shifted upward in altitude, because we found the association to be common at altitudes between 60 and 150 m. The successful spread of *L. leucocephala* to higher altitudes may have promoted the invasion of *P. maximum* via the amelioration of soil and water conditions. Many genetically selected varieties and chromosomal variants (Wagner et al. 1990) of *P. maximum* have been imported into Hawai'i, and it is also possible that the recent spread of *P. maximum* could also be due to new, more drought-tolerant varieties of this forage plant. It is interesting to note that based on data available in the 1960s, Kartawinata and Mueller-Dombois (1972) correctly predicted the possibility of a vegetational shift from pili grass to *P. maximum*–*L. leucocephala*, but their analysis did not predict the shift from pili grass to *C. ciliaris* or *P. setaceum*, despite the presence of these species on O'ahu during the 1960s.

Curiously, a fourth African grass that Kartawinata (1971) almost always found associated with pili grass, *Rhynchelytrum repens* (natal reedtop), was absent or rare in most of the 1997 plots. Even the sites that remained dominated by pili grass in 1997 usually contained no more than 5% cover by *R. repens*. *Rhynchelytrum repens* has been observed to become increasingly dominant over pili grass with increasing moisture (Kartawinata and Mueller-Dombois 1972). During the period from 1965 to 1967, immediately preceding Kartawinata's surveys, annual rainfall (as measured at Honolulu International Airport) averaged one-third higher than in the 3 yr immediately preceding our 1997 survey (Anonymous 1997). Perhaps lower rainfall in the years preceding our survey led to a decline of *R. repens* within the pili grass communities.

Decline in Diversity

Recently established communities dominated by African grasses were significantly less diverse than the former pili grass-dominated communities. This may be due to

the denser growth of the invasive grasses, which may crowd out competing species, relative to the more open growth of pili grass (Mueller-Dombois 1981). Putative native species found at least occasionally in pili grass-dominated communities have included *Sida fallax*, *Eragrostis variabilis*, *Digitaria setigera*, *Panicum torridum*, *Boerhavia repens*, and *Doryopteris decipiens*.

Decline of Pili Grass on Other Islands

Although our quantitative data on pili grass decline are from O'ahu only, we also visited sites on the island of Hawai'i and observed a similar recent pili grass decline there. North of Kona, we visited sites near Kohala Mountain that had been recorded as being a mixture of pili grass and *C. ciliaris* within the last 10 yr (McEldowney 1983; L. Pratt, Hawai'i Volcanoes National Park, pers. comm.). During searches of the area in 1997, we rarely encountered pili grass, and in the few places that we did find it, it occurred as scattered small populations. *Cenchrus ciliaris* dominated all sites. In another survey, we visited sites south of Kona, near Pu'u Honua O Hōnaunau National Historic Park, where pili grass was formerly common (V. Bio, Pu'u Honua O Hōnaunau National Historic Park, pers. comm.), and we could locate only three pili plants. Those sites are now dominated by *L. leucocephala* and *R. repens*. Finally, even at Hawai'i Volcanoes National Park, which still has a comparatively large coastal lowland population of pili grass below the Hōlei Pali and Hilina Pali, there has been concern in recent decades about the increasing dominance of alien grasses in the area, and the spread of these alien grasses has been associated with a corresponding decline in pili grass over large areas there (Vogl 1969). Both pili grass and the invasive African grasses are fire-adapted, but are now growing in areas where fires are largely suppressed by human intervention. Research is needed to determine how fire influences competitive interactions between pili grass and invasive species. Perhaps application of a controlled fire regime could be used as a management tool in maintaining or restoring

the rapidly declining pili grasslands, along with their associated higher floristic diversity and cultural value in the Hawaiian Islands.

ACKNOWLEDGMENTS

Kaliko Amona, Erin Goergen, Curtis Ewing, and Louis Santiago provided valuable field assistance. We thank G. Carr and D. Mueller-Dombois for comments on the manuscript.

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APPENDIX
LOCATIONS, COORDINATES, AND ATTRIBUTES OF PLOTS

SITE NO.	LOCATION	LATITUDE	LONGITUDE	ALTITUDE (m)	SLOPE (degrees)	EXPOSURE
1	Koko Head	21° 15' 55"	157° 42' 45"	6	10	W
2	Koko Head	21° 15' 55"	157° 42' 35"	40	20	W
3	Koko Head	21° 15' 55"	157° 42' 33"	69	25	W
4	Koko Head	21° 15' 55"	157° 42' 30"	106	25	W
5	Koko Head	21° 15' 55"	157° 42' 25"	116	35	W
6	Koko Head	21° 15' 55"	157° 42' 20"	166	35	W
13	Koko Head	21° 15' 57"	157° 42' 28"	106	25	W
30	Ka'ena Point	21° 34' 32"	158° 16' 36"	36	40	S
43	Mākaha	21° 29' 13"	158° 13' 30"	61	40	SE
44	Mākaha	21° 29' 32"	158° 13' 29"	61	40	NE
45	Pu'u Kamaile'unu	21° 27' 05"	158° 12' 00"	55	30	NW
46	Pu'u Kamaile'unu	21° 27' 03"	158° 12' 02"	55	30	S
47	Pu'u O Hulu Uka	21° 24' 20"	158° 09' 42"	153	25	NW
48	Pu'u O Hulu Uka	21° 24' 20"	158° 09' 44"	151	35	NW
49	Kahe Point	21° 21' 22"	158° 07' 39"	70	25	NW
50	Kahe Point	21° 21' 21"	158° 07' 40"	70	25	NW
53	Wa'ahila Ridge	21° 18' 00"	157° 48' 55"	69	10	S
55	Ka'ena Point	21° 34' 40"	158° 16' 13"	50	45	N
58	Ka'ena Point	21° 34' 40"	158° 15' 15"	60	45	NW
64	Makapu'u Hill	21° 18' 25"	157° 38' 37"	100	25	SW
65	Makapu'u Hill	21° 08' 27"	157° 38' 23"	100	25	SE
73	Koko Crater	21° 17' 05"	157° 41' 09"	200	30	S
78	Makapu'u Hill	21° 18' 20"	157° 38' 25"	50	30	S
79	Makapu'u Hill	21° 18' 23"	157° 38' 22"	55	45	SE
80	Makapu'u Hill	21° 18' 18"	157° 38' 20"	35	30	SE
81	Makapu'u Hill	21° 18' 20"	157° 38' 20"	50	35	SE
89	Koko Crater	21° 17' 03"	157° 40' 52"	20	25	SW
91	Ka'iwa Ridge	21° 23' 17"	157° 43' 05"	181	30	E
92	Ka'iwa Ridge	21° 23' 15"	157° 43' 10"	164	35	SW
93	Diamond Head	21° 15' 35"	157° 48' 35"	60	30	S
94	Diamond Head	21° 15' 35"	157° 48' 33"	60	25	S
96	Kahe Point	21° 21' 35"	158° 07' 25"	114	15	S
97	Kahe Point	21° 21' 18"	158° 07' 28"	111	20	SE
98	Kahe Point	21° 21' 15"	158° 07' 33"	121	30	E
99	Kahe Point	21° 21' 30"	158° 07' 35"	121	20	N
100	Kahe Point	21° 21' 15"	158° 07' 48"	80	25	SW
101	Ka'iwa Ridge	21° 23' 07"	157° 43' 15"	144	30	S
102	Ka'iwa Ridge	21° 23' 05"	157° 43' 10"	143	30	NW
103	Pu'u O Hulu Uka	21° 24' 15"	158° 09' 45"	70	30	SW
104	Pu'u O Hulu Uka	21° 24' 15"	158° 09' 42"	71	35	S
105	Pu'u O Hulu Kai	21° 24' 15"	158° 09' 55"	101	35	SE

*Modified from original figure given in Kartawinata (1971) to correct for typographic errors or presumed addition/subtraction errors.